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Seeking consensus on main categories of ecological strategies of earthworms

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SUMMARY

There is no general agreement on acceptability nor precise interpretation of ecological strategies of earthworms. Working in New Zealand, Lee (1959) categorized a dozen species habitat types as aquatic, arboreal or terrestrial, with special emphasis on those in the soil that he divided into: Litter, Topsoil or Subsoil. Bouché's (1977) equivalent categories for French lumbricids were: Epigeés, Anéciques (from Greek "reaching up"), and Endogées. Many students ignore priority and use the French terms despite several authorities preferring Lee's terms (sometimes with Bouche's equivalents appended) or, more recently, modifying these by dividing worms into behavioral classes such as "litter-dwellers", "shallow soil dwellers" and the "deep-burrowers". For practical purposes and reasons of priority, it is reasonable to support Lee's ecological categories based on their easily recognized soil horizon habitat, combined with Bouché's single term "anécique" (Anglicized to anecic) for the relatively few species that maintain

(semi-?)permanent vertical or U-shaped burrows allowing them to feed on litter at the surface. In conclusion, the categories are: 1/. **Litter species**, including the "vermicomposting species"; 2/. **Topsoil species**, including the "fieldworking worms"; 3/. **Subsoil species** living and feeding mainly in the deeper mineral layers of soil that are consequently more difficult to sample and are often underestimated; and 4/. **Anecic species** a special case for species living in the mineral soil but foraging (and mating) on the surface, for which relatively few examples are available.

INTRODUCTION

In addition to taxonomic identification of species, ecological classification of earthworms is required for studies of their various lifestyles and functions, the usefulness of which relates to their vital importance for recycling organic matter (including organic carbon) and maintaining soil structure for crops.

Earthworms' ecological strategies reflect patterns of behaviour, morphology, physiology, phenology, demography, and habitat, and have been classified by various authors. Most notably, Lee (1959, 1985, 1987) categorized New Zealand's species, that were at that time amongst the most biodiverse, and subsequently and independently Bouché (1971, 1972, 1977) studied French lumbricids, the latter scheme extended to West African species by Lavelle (1978, 1979, 1983). Lee (1985) and Edwards & Bohlen (1996) and Blakemore (2002) provide comprehensive reviews and discussion on the ecology of earthworms and their relationship with soils and land use.

Based on broad eco-taxonomic studies of New Zealand earthworms, Lee (1959: 418) proposed readily interpretable categories that are applicable to most earthworms, although these may change with the life-stage of the worm; these were:

Terrestrial	
	soil, including leaf mould (humus)
	under logs and stones on soil surface
	under the bark of dead trees; in rotting logs
Arboreal	in decaying plant remains in the axils of branches of forest trees
Aquatic	
	in the mud and under stones of stream, pond and lake bottoms
	in the water of deep lakes
	in swamps
Littoral	in the intertidal zone on sea shores and adjacent brackish water

Lee argued that the most successful habitat was in soil, and his major categories were:

1. **Litter (or leaf mould) species** – live and feed in the rich litter layers on the soil surface and are subject to greater environmental fluctuations and predation.
2. **Topsoil species** – maintain burrows in the A-horizon, only occasionally coming to the surface to feed (or mate).
3. **Subsoil species** – dwell entirely underground in extensive burrows in the B and/or C horizons of the soil feeding in the lower root zones.

Presumably, most of the subsoil species breed entirely underground as with *Megascolides australis* McCoy, 1878 the "Giant Gippsland Earthworm" from southern Victoria (vanPraagh, 1992). Others may also provide the intermittently observed phenomenon of mass migration where large species are observed on the surface under suitable conditions e.g. for *Vesiculodrilus glandiferus pyengana* Blakemore, 2000 and *Vesiculodrilus tasmanianus* (Fletcher, 1887), see also Stephenson (1930) and Reddy (1980) noting mass migration of geophageous *Amynthas alexandri* Beddard, 1901.

Gates (1961) classified lumbricids in Maine, USA into ecological groups based on their seasonal activity, habitat and diet as:

1. *Geophagous* - feeding mainly on soil.
2. *Limicolous* (or *limiphagous*) - in mud or saturated soils.
3. *Litter feeders* - in leaf litter, compost or manure.

Bouché's (1971, 1977) subsequent scheme, most applicable to a relatively fewer French lumbricids, was:

1. **Epigeés –** living and feeding on the soil surface (this term is actually adopted from plant and other invertebrate glossaries, the opposite perhaps being "hypogaeic") (equivalent to Lee's litter species group).
2. **Anéciques** – relatively rare situation where a worm burrows into the soil in A to C horizons but feeds at the surface (from Greek meaning to "reach up") (most species would be classified as topsoil species in Lee's classification, but some make deeper burrows and might be included with subsoil species).
3. **Endogées** – live in the mineral horizons, feeding on organic matter in the soil, with sub-categories depending on depth of working (equivalent to Lee's topsoil and subsoil species).

The terms "epigeic" (or epigean or epigaen or epigenous) - meaning living at or above the soil surface, and "endogeic" (or euedaphic or hypogeic) - meaning interstitial soil dwellers, are also used in a similar way by some other branches of soil ecology; whereas "anecic", from Greek *anekas* meaning upwards (reaching), appears to be used only for deep burrowing earthworms that come to the surface to feed and breed.

The three classificatory schemes above are essentially complementary in their parameters, differing slightly in interpretation, although Lee's prior terms take precedence

and largely encompass the equivalent French terms and have the added advantage of avoiding exclusive technical terms that obscure general understanding. Lee (1985; 1987) further related ecological survival and reproductive strategies of earthworms to the concepts of "r-, K- and A-selection" and to the habitat templet of Southwood (1977).

Several respected authorities, e.g. Sims & Gerard (1985; 1999: 29-30) in UK and Coleman & Crossley in USA (1996; 2003: 104, Tab. 4.6) list Lee's terms (with Bouché's equivalents appended or in braces). Blakemore (1994; 2002) followed Lee (1985) as essentially did Kladivko (1997) who divided worms into three major behavioral classes: "litter-dwellers", "shallow soil dwellers" and the "deep-burrowers" (see also Anonymous, 2007). However, several species appear to overlap categories, are intermediate, differ with their life stage, or fail to comply with any of the above categories indicating a need for further refined classification. For example *Metaphire musica* (Horst, 1883) lives in leaf axils of epiphytic tree fern (*Asplenium* spp), apparently one pair of matures per fern (Hari Nugroho pers. comm. April, 2006) while the habitat of the immatures is less certain.

Perel (1977) divided Russian lumbricids into 'humus feeders' and 'humus formers' which corresponds closely with detritivores that feed directly on organic substrates, and geophages that feed on organic matter incorporated in the soil. Whereas, Buckerfield (1994) greatly simplified classification of commonly encountered earthworms as either 'composters' or 'fieldworkers'. Species used in vermiculture and vermicomposting are mostly derived from litter species and are classed as 'composters'; these species can be readily cultured in rich organic substrates but in general do not survive well in the field, and are not the same as the most beneficial of agricultural and horticultural 'fieldworkers'. Vermiculture and vermicomposting are expanding industries for which success of operation

depends on selection of appropriate behavioural and ecological characteristics of stock and, as prerequisite, correct species identification and ecological classification.

MATERIALS AND METHODS

The ecological strategies of earthworms briefly reviewed above are adapted, following the scientific conventions of priority, for the most appropriate and generally applicable terms as advocated below. Summary of the characteristics, behaviours and examples for the various groups are presented in order to stimulate discussion on further refinement of suitable habitat templets.

RESULTS AND DISCUSSION

Of the various schemes presented and referenced, for practical purposes following the Scientific Principle of Priority of publication, it appears preferable to support Lee's (1959) ecological categories based on their easily recognized soil horizon habitat, combined with Bouché's (1971) single term "anécique" for the very few species that maintain (semi-?)permanent vertical or U-shaped burrows allowing them to feed on litter at the surface and also to forage and breed there. Examples of species complying with the various categories, many of which are cosmopolitans, are given in Blakemore (2002) although, in general, the higher taxonomic category (family:genus) does not correspond entirely to the ecological one.

Thus a reasonable summary of the major earthworm Ecological Strategies (Fig. 1) is:

1. **Litter species**, including "vermicomposting species", such as *Eisenia fetida* (Savigny, 1826) or *Didymogaster sylvatica* Fletcher, 1886.
2. **Topsoil species**, often the "fieldworking worms", such as *Aporrectodea*

caliginosa (Savigny, 1826), *A. trapezoides* (Dugès, 1828) or *Anisochaeta macleayi* (Fletcher, 1889).

3. **Subsoil species** living and feeding mainly in the deeper mineral layers of soil that are more difficult to sample, e.g. in Australia *Megascolides australis*, *Vesiculodrilus tasmanianus*, *Notoscolex grandis* Fletcher, 1886 and several *Digaster* spp. and *Diplotrema* spp. in eastern Australia (Blakemore, 1994, 1997).
4. **Anecic species** such as *Lumbricus terrestris* Linnaeus, 1758, *L. polyphemus* (Fitzinger, 1833) or *Amynthas yambaruensis* on Okinawa.

Lee's other categories encompassed a wider repertoire of behaviours and habitats, for example species that are aquatic (e.g. *Biwadrilus* or *Eiseniella* spp.), arboreal (e.g. *Planapheretima* spp), or littoral (e.g. *Pontodrilus* spp.).

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REFERENCES

Anonymous (2007). The Massey University, N.Z. website that summarizes Lee's groups: http://soilbugs.massey.ac.nz/oligochaeta.php.

Blakemore, R.J. (1994). *Earthworms of south-east Queensland and their agronomic potential in brigalow soils.* PhD. Thesis, University of Queensland. Pp 605 with the description of 75 species, including 80 figures.

Blakemore, R.J. (1997). Two new genera and some new species of Australian earthworms (Acanthodrilidae, Megascolecidae: Oligochaeta). *Journal of Natural History*. **31**: 1785-1848.

Blakemore, R.J. (2000). *Tasmanian Earthworms*. CD-ROM Monograph with Review of World Families. 'VermEcology', PO BOX 414 Kippax 2615. Canberra, December, 2000. Pp. 800 including 222 figures. ISBN 0-646-41088-1. [http://www.nrel.colostate.edu/IBOY/australia_ap.html#earthworms].

Blakemore, R.J. (2002). *Cosmopolitan Earthworms – an Eco-Taxonomic Guide to the Peregrine Species of the World*. VermEcology, PO BOX 414 Kippax, ACT 2615, Australia. Pp. 426 including 80 figs.

Bouché, M.B. (1971). Relation d'entre les structures spatiales et fonctionelles des écosystms illustrées par le role pédobiologique des vers de terre. In: C. Delamere Bebouttevillle (ed.). *La Vie dans les Sols*. Gauthiers Villars, Paris. Pp. 189-209.

Bouché, M.B. (1972). *Lombriciens de France. Écologie et Systématique*. INRA Publication. 72-2. Institut National des Recherches Agriculturelles, Paris. Pp 1-671.

Bouché, M.B. (1977). Stratégies lombriciennes. In: U. Lohm and T. Persson. (eds.) *Soil Organisms as Components of Ecosystems. Biological Bulletin.* **25:** 122-132.Kladivko, E.J. (1997). Earthworms and Crop Management. Purdue University website: http://www.ces.purdue.edu/extmedia/AY/AY-279.html.

Buckerfield, J.C. (1994). Appropriate earthworms for agriculture and vermiculture. *Technical Memoir.* **2/1994**, CSIRO Soils, Adelaide.

Coleman, D.C. and Crossley, D.A. (1996; 2003). *Fundamentals of Soil Ecology*. (Vol. 2). AP, UK. Pp. 205.

Edwards, C.E. and Bohlen, P.J. (1996). *Biology and Ecology of Earthworms*. Chapman & Hall, London. Pp. xii + 426.

Gates, G.E. (1961). Ecology of some earthworms with special reference to seasonal activity. *American Midland Naturalist.* **66:** 61-86.

Kladivko, E.J. (1997). Earthworms and Crop Management. Purdue University website: http://www.ces.purdue.edu/extmedia/AY/AY-279.html.

Lavelle, P. (1978). Les vers de terre de la savane de Lamto (Cote d'Ivoire). Peuplements, populations et fonctions dans l'ecosysteme. *Publications du Laboratoire de Zoologie de l'École Normale Supérieur, Paris.* No. 12. Pp 301.

Lavelle, P. (1979). Relations entre types ecologiques et profils demographiques chez les vers de terre de la savane de Lamto (Cote d'Ivoire). *Rev. Ecol. Biol. Sol.* **16:** 85-101.

Lavelle, P. (1983). The structure of earthworm communities. In: Satchell, J.E. (ed.) *Earthworm Ecology*. Chapman & Hall, London. Pp 449-465.

Lee, K.E. (1959). *The Earthworm Fauna of New Zealand*. New Zealand Department of Scientific and Industrial Research, Wellington. Bulletin 130. Pp 486.

Lee, K.E. (1985). "Earthworms - Their Ecology and Relationships with Soils and Land Use". Academic Press, Sydney. Pp 411.

Lee, K.E. (1987). Ecological strategies of earthworms. In: Bonvicini Pagliai, A.M. and Omodeo, P. (eds.). *On Earthworms*. Selected Symposia and Monographs. U.Z.I., 2, Mucchi, Modena. Pp. 171-181.

Perel, T.S. (1977). Differences in umbricid organisation connected with ecological properties. In: Lohm U. and Persson, T. (eds). *Soil Organisms as Components of*

Ecosystems. *Biol. Bull. (Stockholm).* **25:** 56-63.

Reddy, V. (1980). Mass migration and mortality of *Amynthas* (= *Pheretima*) *alexandri* (Beddard). *Proceedings of the Indian Academy of Science*. **49(15):** 606. [http://www.ias.ac.in/j_archive/currsci/49/15/606-606/viewpage.html].

Sims, R.W. and Gerard, B.M. (1985; 1999). *Earthworms: Notes for the identification of British species*. 4th Edition. Published for The Linnean Society of London and The Estuarine and Coastal Sciences Association by Field Studies Council, Montford Bridge, Shrewsbury, UK. Pp. 169.

Southwood, T.R.E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology.* **46:** 337-365.

Stephenson, J. (1930). *The Oligochaeta*. Oxford University, Clarendon Press. Pp. 978.

vanPraagh, B. (1992). The biology and conservation of the Giant Gippsland earthworm *Megascolides australis* McCoy, 1878. *Soil Biology & Biochemistry.* **24(12):** 1363-1369.

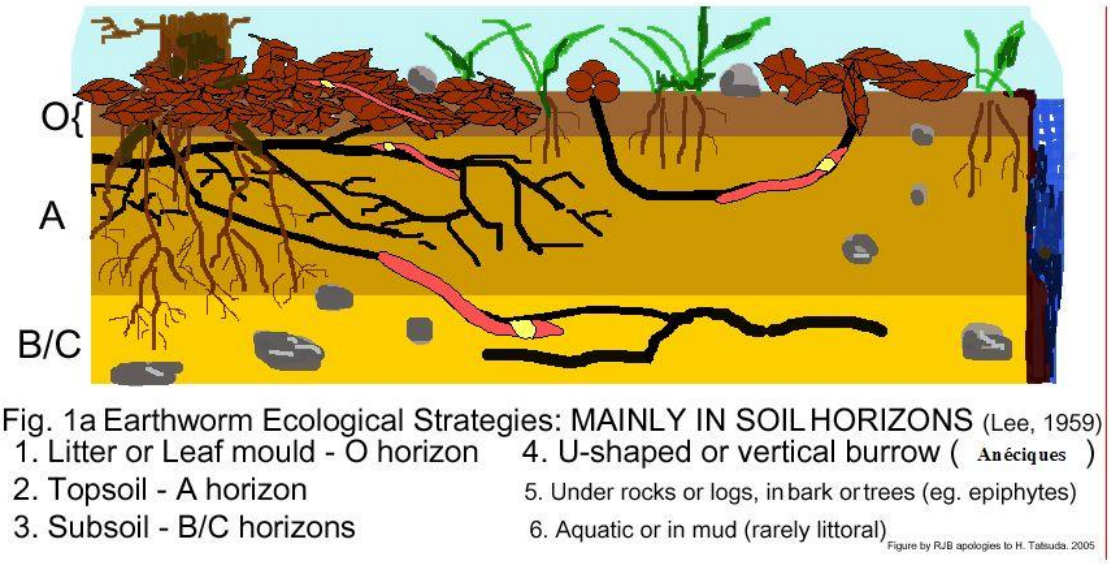

Figure 1. Schema of the four main Ecological Strategies of earthworms:

1. **Litter** or Leaf Mould (= compost) species of the soil surface O horizon.
2. **Topsoil** species of the soil A horizon (the humic layer).
3. **Subsoil** species of the soil B/C horizons (often, if not always, geopageous).
4. **Anecic** species largely feeding on the surface but dwelling below-ground.

[Figure modified with permission from H. Tatsuta of Yokohama National Uni. (2005)].